



Decadal-scale changes in the community structure of coral reefs of St. John, US Virgin Islands

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ABSTRACT: Most coral reefs differ from those visited by explorers in the 15th century and described by ecologists in the 1950s, and reports of degraded reefs and hypotheses regarding the implications of the changes abound. Tests of these hypotheses require decadal-scale ecological analyses, yet data to support these efforts remain rare. In this study, 25 yr of time-series analyses from 3 habitats in St. John, US Virgin Islands, revealed changes in coral community structure that are spatially and temporally heterogeneous, only loosely coupled with local disturbances, and equivocal in terms of the coral community structure that can be projected from the recent past. In a near-shore habitat at 7 to 9 m depth, coral cover remained ~4% between 1992 and 2011, and variation in benthic community structure was driven mostly by *Agaricia*. In an *Orbicella annularis* (formerly *Montastraea annularis*)-dominated habitat at 9 m depth, coral cover declined from 45% in 1987 to 7% in 2011, and varied among decades. In a second *O. annularis*-dominated habitat at 14 m depth, coral cover increased from 32% in 1987 to 49% in 2002, but then declined to 29% in 2011. The density of small corals also changed between 1994 and 2011, beginning with a density (colonies per 0.25 m²) of 3.5 in 1992, rising to 4.9 in 2005, but declining to 3.0 in 2011. Each genus of small corals responded in dissimilar ways over time, with genera waxing and waning in abundance on multiple occasions and in asynchronous patterns. The reefs of St. John have changed markedly since 1987, but the present results show how adjacent habitats and sympatric coral taxa translate similar environmental signals into discordant community trajectories that suggest that these coral communities will not disappear in the short term.

KEY WORDS: Decadal · Coral reefs · Community structure · Scleractinia

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INTRODUCTION

Human disturbances are evident in every major biome (Woodruff 2001, Parmesan & Yohe 2003), the scale of which has prompted the use of 'Anthropocene' to describe the current geological epoch (Crutzen 2002). Changes associated with the Anthropocene began in the late 18th century (Crutzen 2002), with subsequent effects arising from processes operating over multiple spatio-temporal scales (Crutzen 2002, Steffen et al. 2007). Retrospectively, it is difficult to quantitatively partition the biological signals arising from these processes to multiple causal agents. For instance, global climate change (GCC) caused by increasing atmospheric CO₂ is driv-

ing perturbations in ecosystem structure and function (Parmesan 2006, Burrows et al. 2011), but superimposed on these effects are local disturbances (Parmesan & Yohe 2003) with outcomes that can be similar to those attributed to GCC.

Syntheses of ecological data are powerful tools in quantifying the biological effects of GCC and ocean acidification (OA) (Kroeker et al. 2010, Richardson et al. 2012) and their conclusions are effective in articulating globally coherent messages (e.g. Parmesan & Yohe 2003). However, implicit in their value is a depreciated importance of local-scale detail. While this is a reasonable compromise for many messages, such as conveying the biological gravity of GCC and OA (Parmesan & Yohe 2003, Doney et al. 2012), in

other cases it is the detail that provides context to the generality. For example, ecological refugia (sensu Pielou 1979) create the potential for survival of denuded populations (Keppel et al. 2012). Rare records of stable or upward population trajectories indicate exceptions to the broader signs of population decline (Moore & Barlow 2011, De'ath et al. 2012), and it is the survivors of epidemics that fuel subsequent population recovery (O'Brien & Evermann 1988). Coral reefs provide an interesting example of the aforementioned principles, for while they have long been valued as the tropical rainforests of the sea (Connell 1978), in recent years they have been used as symbols of ecosystem collapse (Aronson & Precht 2001, Bellwood et al. 2004), even while a small number apparently continue to thrive (Sandin et al. 2008, Sheppard et al. 2008).

Global trends for changes in coral reef community structure

There are nuances to the changes in community structure that have occurred on coral reefs (Bruno & Selig 2007), but the consistent theme includes reduced abundances of vertebrate predators and grazers, declines in coral cover, reduced reef complexity, and increased cover of macroalgae (Jackson 1977, McCook 1999, Bellwood et al. 2004, Alvarez-Filip et al. 2009). Surprisingly, however, describing the changes that have affected coral reefs, as well as elucidating the drivers of these changes and projecting the likely outcomes, has been contentious (Hughes et al. 1999, Bruno et al. 2009, Mumby et al. 2012). It was disturbances such as hurricanes in the 1980s that first brought attention to the possibility that coral reefs could transition to an alternative phase dominated by macroalgae (Lighty 1982, Hatcher 1984, Hughes et al. 1987), and by the early 1990s, the concept of a phase change on coral reefs was receiving widespread attention (Done 1992). While it was suggested that this transition represented an alternative stable state (Knowlton 1992, Nyström et al. 2000, Mumby 2009), it is better considered as a change in phase, because the alternative state persists under a set of external conditions differing from those favoring the dominance of coral (Dudgeon et al. 2010, but see Mumby et al. 2012). While early opinions differed regarding the theoretical interpretation of a switch to macroalgal dominance on coral reefs, and its causes (Hughes et al. 1999), acceptance of the phase-change concept was favored in the 1990s by numerous examples of declines in

coral cover together with increases in macroalgal cover (Ginsburg 1994, Karlson & Hurd 1993, Hughes 1994), notably as a result of coral bleaching (Glynn 1993, Hoegh-Guldberg 1999) and coral diseases (Aronson & Precht 2001, Harvell et al. 2004). In the 21st century, pessimism over the future of coral reefs has continued to deepen as appreciation of the threats posed by GCC and OA has intensified (Hoegh-Guldberg et al. 2007, Doney et al. 2009).

Amid the gloomy prognoses for coral reefs, a few corals have emerged as at least temporary ecological winners while other corals around them have died (Loya et al. 2001, Fabricius et al. 2011). Such evidence demonstrates that scleractinian corals are not affected equally by environmental challenges, and raises the possibility that some might endure contemporary assaults (Hughes et al. 2003, Pandolfi et al. 2011), at least in the short term. In addition to signs that coral taxa display heterogeneous responses to similar disturbances, questions have emerged regarding the commonality of trajectories of change in coral reef community structure (Schutte et al. 2010, Osborne et al. 2011), as well as the generality of the phase transition from coral to macroalgae dominance and the inverse relationship between coral cover and macroalgal cover (Bruno et al. 2009). While the biological significance of these apparent exceptions to the general trends affecting coral reefs remains to be determined, they underscore the importance of detail-oriented studies to the broader context of coral reef community ecology.

Coral reefs in the US Virgin Islands

In the Caribbean, one region with a long history of marine ecological investigation is the US Virgin Islands (Rogers et al. 2008), where one island, St. John, is mostly protected by the Virgin Islands National Park (VINP) and a Biosphere Reserve (Rogers & Teytaud 1988). The ecology of coral reefs surrounding St. John was first described quantitatively by John Randall in the 1950s (e.g. Randall 1961), scientists in the Tektite undersea laboratory in the late 1960s (Collette & Earle 1972), and the VINP and the present author since the late 1980s (Rogers & Beets 2001, Rogers et al. 2008). Most of this work focused on shallow reefs around Great Lameshur Bay on the south coast. In this location, coral reefs closest to shore occur as a veneer on igneous rock to about 9 m depth, and seaward they form large patches of mostly *Orbicella annularis* (formerly *Montastraea annularis*; Budd et al. 2012), forming carbonate frameworks to at least

20 m depth (Rogers et al. 2008). In the 1960s, these reefs were flourishing with high coral cover (Collette & Earle 1972, Lee et al. 1975), and as recently as the mid-1980s, at least one area had 45% coral cover (Edmunds 2002). Rigorous ecological monitoring of these reefs began in 1987 (Edmunds & Witman 1991, Edmunds 2002), and multiple disturbances occurred over the following 25 yr (Rogers et al. 2008, P. J. Edmunds unpubl.). As a result of these (and many other) effects, the shallow coral reefs of St. John (and the US Virgin Islands overall) generally have lower coral cover today than they had 25 yr ago (Rogers et al. 2008, P. J. Edmunds pers. obs.). As is described below, however, over a spatial scale of <10 km, the patterns of change in coral reef community structure are less clear, more heterogeneous, and not coupled simply to single causal processes.

The objectives of this study were to describe 25 yr of coral reef community dynamics in shallow habitats along ~10 km of shore between Cabritte Horn and White Point on the south shore of St. John. The study was initiated in 1987, and the results have supported investigations focused on the population and community ecology of scleractinian corals, with the last description of coral reef community structure covering 1987 to 1998 (Edmunds 2002). Here, I revisit the changes in coral reef community structure that occurred during the first decade of this study, and use them to contextualize the changes observed in the second and part of the third decade of this study. In addition to the greater ecological relevance provided by 25 yr of data in elucidating meaningful changes in coral reef community structure, I used this dataset to address 3 questions. (1) Are the trajectories of change in coral community structure consistent among habitats? (2) To what extent are changes in coral community structure in dissimilar habitats modulated by the same disturbances? (3) What can 25 yr of coral reef community dynamics say about the likely future of coral reefs in this location?

MATERIALS AND METHODS

Overview

The shallow reefs of St. John were censused annually in 3 habitats beginning as early as 1987 (Fig. 1). Surveys were completed in December 1987, March 1988, July 1988, December 1988, April 1989, October 1989, March 1991, May 1992, June 1993, August 1994, May 1995 to 1997, and July or August thereafter. In

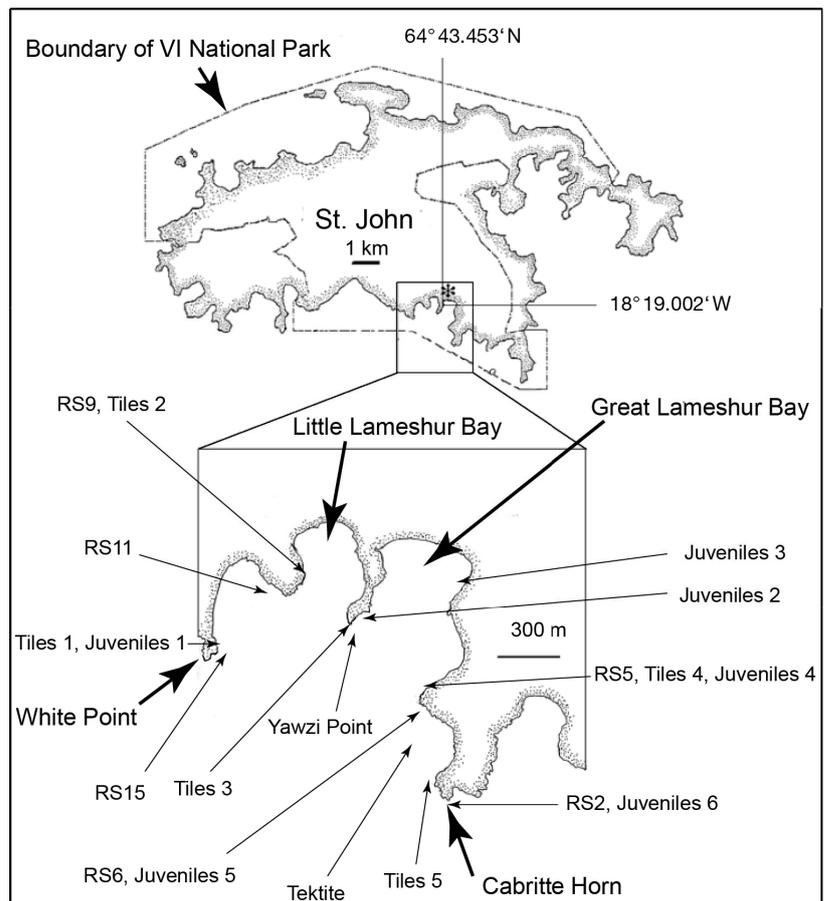


Fig. 1. Map of St. John showing study sites between Cabritte Horn and White Point that were used for (1) sampling benthic community structure through photoquadrats in 3 habitats (Yawzi Point, Tektite, and random sites [RS], pooled and analyzed as PRS), (2) censusing juvenile corals (≤ 40 mm diameter) (Juveniles 1–6), and (3) evaluating coral recruitment (Tiles 1–5). Depths and coordinates are (a) Yawzi Point, 9 m, N18° 18.912', W064° 43.500'; (b) Tektite, 14 m, N18° 18.582', W064° 43.371'; (c) RS sites, 7–9 m, RS2 = N18° 18.404', W064° 43.308', RS5 = N18° 18.760', W064° 43.383', RS6 = N18° 18.682', W064° 43.368', RS9 = N18° 19.028', W064° 43.667', RS11 = N18° 18.976', W064° 43.783', and RS15 = N18° 18.910', W064° 43.967', (d) juvenile sites, 6 at 5 m, Juvenile 1 = N18° 18.880', W064° 43.895', Juvenile 2 = N18° 18.935', W064° 43.506', Juvenile 3 = N18° 18.997', W064° 43.270', Juvenile 4 = as for RS5: Juvenile 5 = as for RS6, and Juvenile 6 = as for RS2, (e) tile sites, 5–6 m, Tile 1 = as for Juvenile 1, Tile 2 = as for RS9, Tile 3 = N18° 18.909', W064° 43.559', Tile 4 = as for RS5, and Tile 5 = N18° 18.521', W064° 43.327'. Asterisk marks the Virgin Islands Ecological Resource Station (VIERS)

1987, one habitat was sampled at Yawzi Point (9 m depth) and another at Tektite (14 m depth), and both consisted of dense aggregates of *Orbicella annularis*. These sites were used to evaluate the effect of coral bleaching in 1987, and were chosen because they were known locally for high coral cover. To address the bias created by this choice (Hughes 1992, Rogers 1999), 6 additional sites were added in 1992 using random coordinates constrained to hard substrata at 7 to 9 m depth between Cabritte Horn and White Point. These sites sampled a habitat closer to shore where boulders and cliffs of igneous rock are common, mean coral cover has remained <5%, and *Orbicella annularis* is rare. Previously, the random sites have been analyzed separately (Edmunds 2002), but here they are analyzed together as 'pooled random sites' (PRS) describing a single habitat. To evaluate the demographic processes affecting coral cover, the density of small corals has been censused since 1994 at 2 to 5 sites at 5 m depth, and one site at 9 m depth.

Benthic community structure

Benthic community structure was quantified using photoquadrats recorded at least annually using cameras attached to strobes and mounted on a framer. Before 2000, pictures were taken with a Nikonos V fitted with a 28 mm lens and Kodachrome 64 film, but in 2000 a digital format was adopted, first with 3.34 megapixels (2000 to 2006) and then 6.1 megapixels resolution. Slides were digitized, and all images and their quantitative analyses were archived (<http://mcr.lternet.edu/vinp/>) (Edmunds 2013). Objects ≥ 1 cm diameter could be resolved.

At Yawzi Point and Tektite, the study areas consisted of 3 parallel 10 m transects at a constant depth, along which 10 contiguous photoquadrats were recorded at each sampling (~30 photoquadrats per year). To capture the scale of a reef dominated by *Orbicella annularis*, 1×1 m photoquadrats were recorded using a camera attached to a strobe (Nikonos SB105) and mounted on a large framer. The PRS were sampled with a smaller photoquadrat (0.5×0.5 m) that was placed at random locations along a fixed transect at each site. Transects were 20 m long and sampled using ~18 photoquadrats per year when film was employed, but 40 m long and sampled with ~40 photoquadrats per year when a digital format was adopted. Photoquadrats at the PRS were recorded using a camera fitted with 2 strobes (Nikonos SB105), and the position of the photoquadrats was randomized at each sampling.

Photoquadrats were analyzed by overlaying them with 200 randomly placed dots, and counting the dots on substrata of interest; 3 substrata were resolved: scleractinian corals, macroalgae, and a combined category of crustose coralline algae, bare space, and turf (CTB, Aronson & Precht 2000). Macroalgae were defined as algae ≥ 1 cm high, and generally consisted of *Halimeda*, *Lobophora*, *Padina*, and *Dictyota*; the CTB category was used because the component groups could not be resolved in planar images (Aronson & Precht 2000, Edmunds 2002). At Yawzi Point and Tektite, *Orbicella annularis* was quantified separately within the Scleractinia because of the importance of this taxon, and at the PRS, scleractinian corals were resolved to genus level. Other than *O. annularis*, species-level resolution is not reported, as either this was not possible due to limited image quality, or because individual species were too rare to quantify with the sampling regime employed. Before 2005, images were analyzed manually, but Coral Point Count with Excel extensions (CPCe) software (Kohler & Gill 2006) was used thereafter. The present study included an evaluation of all data for quality assurance and quality control, and this procedure resulted in the re-analysis of many early images published in Edmunds (2002).

Small corals

Small corals (<40 mm diameter) were censused annually at 2 to 6 sites between Cabritte Horn and White Point, starting in 1994. Small corals were considered to be juvenile colonies, with the rationale that they are not sexually mature at this size (Soong 1993), although this definition required *Favia fragum* and *Siderastrea siderea* to be excluded from the juvenile category as they are sexually mature at ~4 cm diameter (Soong 1993). Small corals were identified to species or genus in 0.5×0.5 m quadrats placed randomly along 40 m transects along the depth contour at either 5 m (5 sites) or 9 m (1 site after 1998) depth; 5 sites were sampled in 1994, 2 in 1995, 5 from 1996 to 1998, and 6 from 1999 to 2011. Results are pooled among sites to describe the density of small corals and the density of juvenile corals by genus.

Statistical analyses

Descriptive statistics (mean \pm SE) were used to display long-term trends in the original units of measure. For benthic community structure and the density

of juvenile corals, non-metric multi-dimensional scaling (MDS; Clarke & Gorley 2006) was used to visualize patterns of similarity over time using multiple dependent variables. Changes in overall community structure as assessed by the mean cover of coral, macroalgae and CTB at Yawzi Point, Tektite, and the PRS was visualized using MDS with square-root transformed data converted to a matrix of Bray-Curtis similarity values. Multiple restarts of 100 iterations were employed until stress stabilized and ordinations were repeatable. The chronology of change in community structure was indicated with a vector linking consecutive samplings, and data were scaled as 'bubbles' reflecting the percentage cover of components of the benthic community. The same techniques were applied to the genus-level PRS coral data, and the genus-level analysis of small coral density. In these cases, data were scaled as bubbles reflecting the abundance of coral genera.

Inferential tests of variation among times were conducted using 1-way ANOSIM (analysis of similarities) with photoquadrats as replicates, and square-root transformed data converted to a matrix of Bray-Curtis similarity values. Following a global test of similarity among times using the R statistic, pairwise contrasts were used to evaluate the periods over which large changes in community structure occurred. Pairwise contrasts were constrained to consecutive years to reduce the likelihood of Type I errors, and differences evaluated using Bonferroni-adjusted probabilities. ANOSIM was applied to (1) the overall community structure at Yawzi Point, Tektite, and the PRS; (2) the genus-level coral analysis of the PRS; and (3) the genus-level analysis of density of small corals.

Univariate contrasts among times were accomplished using repeated measures ANOVA in cases where photoquadrats were sampled repeatedly (Yawzi Point and Tektite); listwise deletion was used where photoquadrats were missing. To compare among times when photoquadrats were randomized at each sampling (PRS and surveys for juvenile corals), 1-way ANOVA was used. ANOVA was also used to compare the density of small corals over time following $\sqrt{(x + 3/8)}$ transformation. Percentage data were arcsine transformed, and planned contrasts among consecutive years accomplished using an F -test with partitioned sums of squares for each contrast (Quinn & Keough 2003). Least squares regression was used to test for linear trajectories of change in the components of benthic community structure.

Statistical analyses were completed using Systat 11.0 (univariate procedures; Systat Software) and

Primer 6.1 (multivariate procedures; Primer-E) running on a Windows 7.0 platform. The statistical assumptions of normality and homoscedasticity were tested through graphical analyses of residuals.

The genus *Montastraea* has undergone a major revision (Budd et al. 2012), with the Caribbean representatives split to *Orbicella* (family Merulinidae: *M. annularis*, *M. franksi* and *M. faveolata*) and *Montastraea cavernosa* (family Montastraeidae). In the present summary of 25 yr of surveys, these corals are combined as '*Montastraea*' with the rationale (as described below) that *M. cavernosa* was rare at the Yawzi and Tektite habitats, *O. annularis* plus *M. cavernosa* covered a small amount of the benthos at the PRS (<2% in all years), and *M. cavernosa* accounted for a mean of only 0.2% of all small corals.

RESULTS

Benthic community structure

At Yawzi Point in 1987, mean coral cover was $44.6 \pm 3.4\%$, macroalgae covered $2.2 \pm 0.4\%$ of the reef, and CTB covered $35.4 \pm 3.7\%$ of the reef (\pm SE, $n = 30$). *Orbicella annularis* represented >77% of the live coral in all survey years, and *Montastraea cavernosa* was rarely encountered. Over 25 yr, community structure changed significantly (ANOSIM, $R = 0.297$, $p = 0.001$), with coral cover decreasing linearly ($F = 205.878$, $df = 1, 25$, $p < 0.001$) at $1.7\% \text{ yr}^{-1}$, and macroalgae and CTB increasing linearly ($F \geq 4.673$, $df = 1, 25$, $p \leq 0.040$) at $1.3\% \text{ yr}^{-1}$ and $0.6\% \text{ yr}^{-1}$, respectively (Fig. 2A). By 2011, mean coral cover was $6.7 \pm 1.7\%$, macroalgae covered $37.7 \pm 2.4\%$ of the reef, and CTB covered $44.2 \pm 2.0\%$ of the reef (\pm SE, $n = 30$). Pairwise contrasts using ANOSIM revealed differences in community structure over 1990–1991 ($R = 0.208$, $p = 0.001$), 1996–1997 ($R = 0.146$, $p = 0.001$), 1997–1998 ($R = 0.156$, $p = 0.001$), and between every other period following August 2000 ($R = 0.138$, $p = 0.001$) except 2007–2008 ($R = 0.001$, $p = 0.332$). MDS revealed shifts in community structure that were characterized by greater differences among years as the study progressed, and losses of coral cover (Fig. 2D). Univariate analysis of coral cover confirmed strong variation over time ($F = 29.714$, $df = 26, 416$, $p < 0.001$), with planned contrasts revealing significant differences between April 1989 and October 1989 ($F = 9.496$, $df = 1, 416$, $p = 0.002$) and over 1988–1989 ($F = 10.920$, $df = 1, 416$, $p = 0.001$); no other contrasts were significant ($p \geq 0.068$).

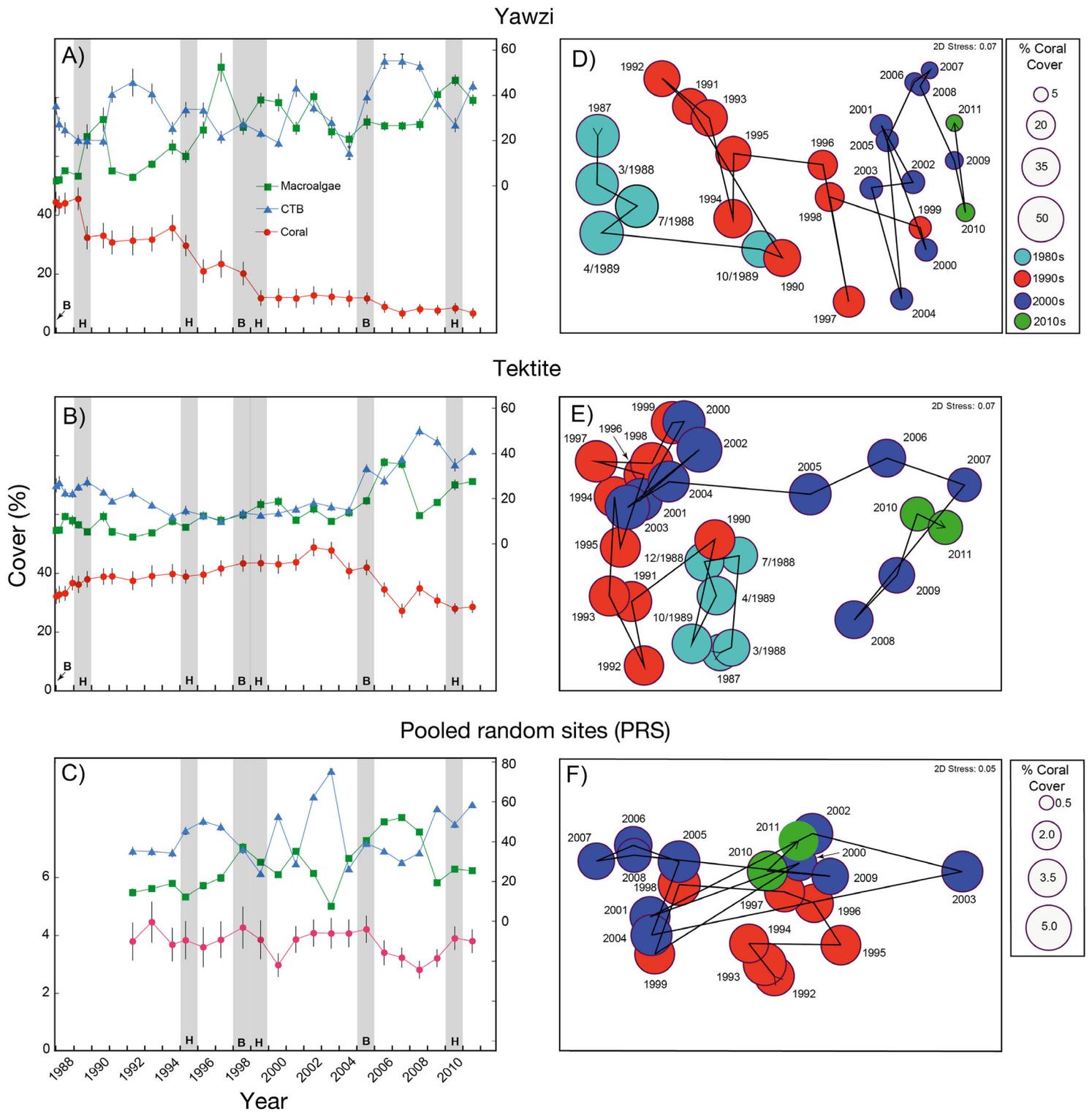


Fig. 2. Benthic community structure over 20 to 25 yr in 3 reef habitats of St. John. (A–C) Percent cover (mean ± SE) of scleractinian corals (left scale), and macroalgae, and crustose coralline algae, algal turf and bare space combined (CTB) (right scale), with sample sizes (number of photoquadrats) of 28 to 30 (Yawzi Point, n = 20 for April 1992), 29 to 30 (Tektite, n = 20 for December 1988 and n = 18 for April 1992), or 97 to 240 (PRS). Gray bars display years affected by bleaching (B) or hurricanes (H). There are no December 1988 data for Yawzi Point. Scales of abscissas differ among graphs. (D–F) Multidimensional scaling (MDS) plots based on 3 categories of benthic community structure (in A–C). Vectors link points based on chronology

Coral reef community dynamics followed a different trajectory at Tektite, ~600 m to the southeast and 5 m deeper. In this habitat, mean coral cover in 1987 was $32.2 \pm 2.5\%$, macroalgae covered $5.9 \pm 0.7\%$ of the reef, and CTB covered $25.8 \pm 3.0\%$ of the reef (\pm SE, $n = 30$) (Fig. 2B). *Orbicella annularis* represented $>72\%$ of the live coral in all survey years, and *Montastraea cavernosa* was uncommon (representing 1.5% of the coral cover in 1987 and 2011). Community structure changed significantly over 25 yr (ANOSIM, $R = 0.279$, $p = 0.001$), but in this habitat coral cover increased linearly from 1987 to 2002 ($F = 105.558$, $df = 1, 17$, $p < 0.001$) at $0.8\% \text{ yr}^{-1}$, before declining at $2.4\% \text{ yr}^{-1}$ ($F = 37.339$, $df = 1, 8$, $p < 0.001$) to end the study at $28.6 \pm 2.0\%$ in 2011 (mean \pm SE, $n = 30$). The cover of macroalgae and CTB increased ($F \geq 7.237$, $df = 1, 26$, $p \leq 0.012$) at $0.8\% \text{ yr}^{-1}$ and $0.6\% \text{ yr}^{-1}$, respectively, but their rates of increase steepened after 2002 to end the study at $27.6 \pm 1.2\%$ (macroalgae) and $40.9 \pm 1.6\%$ (CTB) (mean \pm SE, $n = 30$). Pairwise contrasts using ANOSIM revealed differences in community structure over 2004–2005, 2005–2006, and 2006–2007 ($R \geq 0.265$, $p = 0.001$). MDS revealed slight shifts in community structure from the 1980s to the 1990s, but the changes intensified from 2005 (Fig. 2E). Univariate analysis of coral cover confirmed the variation over time ($F = 7.286$, $df = 27, 459$, $p < 0.001$), with planned contrasts revealing significant differences between December 1988 and April 1989, and over 1991–1992, 2003–2004, 2005–2006, 2006–2007, and 2007–2008 ($F = 3.915$, $df = 1, 459$, $p \leq 0.049$). No other contrasts were significant ($p > 0.076$).

A third pattern of change in community structure occurred at the PRS. Here, mean coral cover remained $\leq 4.5\%$ over 20 yr, and CTB covered 28.9% (2001) to 75.3% (2003) of the reef, although neither changed consistently over time ($F \leq 2.403$, $df = 1, 18$, $p > 0.138$) (Fig. 2C). In contrast, the cover of macroalgae increased from $14.4 \pm 1.7\%$ in 1992, to $25.4 \pm 1.2\%$ in 2011, and was related linearly with time ($F = 5.991$, $df = 1, 18$, $p = 0.025$), increasing at $1.1\% \text{ yr}^{-1}$. Overall community structure changed significantly (ANOSIM, $R = 0.202$, $p = 0.001$), and pairwise contrasts using ANOSIM revealed significant changes over 1993–1994, 1994–1995, 1995–1996, all pairs of years between 1997 and 2006, and over 2008–2009 ($0.637 \geq R \geq 0.020$, $p \leq 0.002$). However, the relative differences in community structure among years were small, as revealed by the clustering in the MDS (Fig. 2F), and the absence of a strong distinction among decades (cf. Fig. 2D).

Unlike the 1×1 m photoquadrats at Yawzi Point and Tektite, the 0.5×0.5 m photoquadrat at the PRS

allowed coral cover to be resolved to genus, although generic-level abundances were low given the sparse coral cover. Of the 20 genera found, 8 were sufficiently abundant to support further analyses (mean cover 0.02 to 1.23%), and collectively, their community structure differed over time (ANOSIM, $R = 0.024$, $p = 0.001$). The genus '*Montastraea*' (*Orbicella annularis* complex and *Montastraea cavernosa* combined) represented 23% (1999) to 47% (2002) of the coral cover (always $< 4.5\%$), with *O. annularis* complex 4-fold more abundant than *M. cavernosa* (pooled among years). Pairwise contrasts of coral community structure using ANOSIM revealed weak changes over time (based on low R values), with the only significant change over 1997 to 1998 ($R = 0.024$, $p = 0.001$). MDS revealed slight changes in community structure that tended to emerge after 1999 and 2005 (Fig. 3). Scaling samplings on the MDS plot as bubbles representing coral cover by genus revealed changes in community structure that were driven largely by *Agaricia*. The cover of *Agaricia* declined 98% from $0.56 \pm 0.11\%$ in 2005 to $0.01 \pm 0.01\%$ in 2007 (both \pm SE, $n = 23$ to 235). Univariate analyses revealed that coral cover did not change over time ($F = 0.875$, $df = 19, 3608$, $p = 0.615$), although the cover of macroalgae and CTB differed among years ($F > 86.077$, $df = 19, 3608$, $p < 0.001$), as did the cover of *Porites*, *Agaricia*, and *Siderastrea* ($F \geq 2.874$, $df = 19, 3608$, $p < 0.001$); the cover of '*Montastraea*' did not change over time ($F = 1.041$, $df = 19, 3608$, $p = 0.408$). Planned contrasts revealed that macroalgae and CTB changed significantly between all pairs of years except 1993–1994, 2006–2007, and 2010–2011 for macroalgae, and 1992–1993, 1994–1995, and 1995–1996 for CTB ($p < 0.050$). For the common coral genera, planned contrasts revealed significant differences ($p < 0.050$) between a few consecutive years for *Agaricia* (2005–2006, 1997–1998, and 1994–1995) and *Porites* (2006–2007 and 2003–2004).

Small corals

Small corals of sexual origin were abundant on hard surfaces in all census years, with densities (corals per 0.25 m^2) $\geq 3.13 \pm 0.23$ (mean \pm SE, $n = 240$). In 1994, the mean density of small corals was 3.47 ± 0.27 ; it reached a maximum of 5.74 ± 0.39 in 2002, and then declined to 3.13 ± 0.23 in 2011 (Fig. 4). Overall, the density of small corals differed significantly among times ($F = 9.399$, $df = 17, 3981$, $p < 0.001$), and planned contrasts revealed significant differences

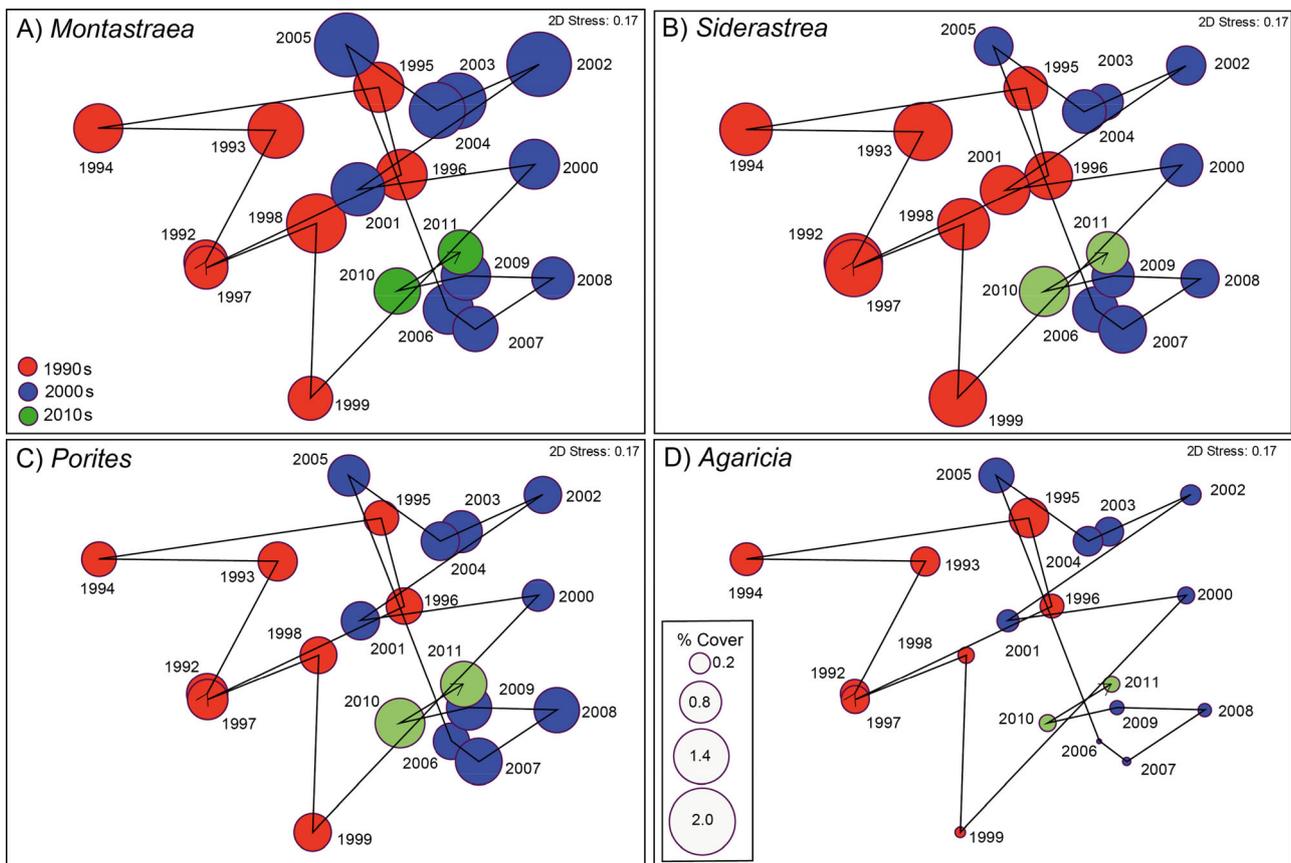


Fig. 3. Multidimensional scaling (MDS) plots showing the generic composition of scleractinian corals at the PRS between 1992 and 2011. Analysis is based on percent cover for 8 genera that accounted for >95% of coral cover: *Montastraea* (*Orbicella annularis* complex and *M. cavernosa* combined; refer to text for further details), *Agaricia*, *Dichocoenia*, *Diploria*, *Meandrina*, *Porites*, *Stephanocoenia*, and *Siderastrea* and the results displayed with bubbles (i.e. years) scaled in diameter to represent the cover of the 4 most common taxa (A–D). Vectors link points by chronology

among consecutive years for 1996–1997, 2005–2006, and 2007–2008 ($F \geq 6.417$, $df = 1,3981$, $p < 0.010$). Densities of small corals were reduced by excluding potentially adult corals (i.e. *Favia fragum* and *Siderastrea radians*). Densities (corals per 0.25 m^2) of juvenile corals varied from 1.62 ± 0.13 in 2011, to 3.09 ± 0.10 in 2005, and were marked by a 39% decline in 2006. Overall, the density of juvenile corals varied significantly over time ($F = 9.810$, $df = 17,2982$, $p < 0.001$), but planned contrasts among consecutive years revealed a significant difference only between 2005 and 2006 ($F = 29.015$, $df = 1,3981$, $p < 0.001$).

For taxa of small corals that were encountered frequently, densities varied over time (Fig. 5) with significant differences for *Agaricia*, *Diploria*, *Favia*, *Porites*, *Siderastrea*, and *S. siderea* ($F \geq 3.927$, $df = 17,3982$, $p < 0.001$), but not '*Montastraea*' ($F = 1.212$, $df = 17,3982$, $p = 0.245$). *Montastraea* (*Orbicella annularis* complex and *M. cavernosa* combined) represented $\leq 0.4\%$ of small corals, and *M. cavernosa*

represented $< 0.2\%$ of small corals. Planned contrasts of small coral densities among consecutive years revealed significant differences for *Agaricia* (2005–2006; $F = 82.702$, $df = 1,3981$, $p < 0.001$), *Favia* (1995–1996, 2001–2004, 2005–2008; $F \geq 4.641$, $df = 1,3981$, $p \leq 0.031$), *Porites* (2007–2008, $F = 11.340$, $df = 1,3981$, $p < 0.001$), *Siderastrea* (1995–1996, 1999–2000, 2005–2007; $F \geq 4.576$, $df = 1,3981$, $p \leq 0.033$); and *S. siderea* (2003–2004, 2006–2007; $F \geq 4.126$, $df = 1,3981$, $p \leq 0.042$). Some of these differences were large, with the density of *Agaricia* declining 90% over 2005–2006, the density of *Favia* increasing 174% over 1996–1997, the density of *Porites* increasing 24% over 2001–2002 and then decreasing 39% over 2007–2008, and the density of *Siderastrea* increasing 104% over 1999–2000 and 44% over 2005–2006, but declining 39% over 2006–2007.

Over the 18 yr study, changes in the densities of small corals conformed to 4 temporal trends: decreases over time, increases over time, consistency

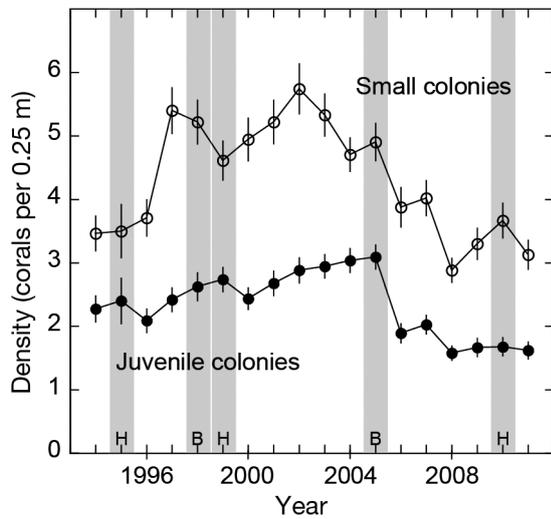


Fig. 4. Density of small corals (colonies ≤ 40 mm diameter) and juvenile corals (≤ 40 mm), excluding *Favia fragum* and *Siderastrea radians* at 5 to 9 m depth between Cabritte Horn and White Point for 18 yr (1994 to 2011). Values pooled among 2 sites (1995), 5 sites (1994, and 1996 to 1998), or 6 sites (1999 to 2011), with $n = 80, 200,$ or 240 quadrats, respectively. Mean \pm SE displayed; gray bars display years affected by bleaching (B) or hurricanes (H)

over time, and those undergoing multiple cycles of increases and decreases (i.e. stability, sensu Holling 1973). Density declined linearly for juvenile *Diploria* ($F = 62.039, df = 1, 17, p < 0.001$) and small *Favia* ($F = 8.657, df = 1, 17, p = 0.009$), which changed at a rate (corals per 0.25 m^2 per decade) of -0.066 ± 0.008 and -0.480 ± 0.163 , respectively; density increased linearly for small *Siderastrea* ($F = 6.528, df = 1, 17, p = 0.021$) and small *S. siderea* ($F = 8.861, df = 1, 17, p = 0.009$), which changed at a rate of 0.361 ± 0.141 and 0.106 ± 0.035 , respectively; density did not change linearly for juvenile *Porites* ($F = 1.625, df = 1, 17, p = 0.220$) and '*Montastraea*' ($F = 2.329, df = 1, 17, p = 0.145$). The density of juvenile *Agaricia* spp. displayed a unique pattern of variation, increasingly linearly between 1997 and 2005 ($F = 9.231, df = 1, 7, p = 0.019$) at a rate of 0.437 ± 0.144 , declining between 2005 and 2006, but again increasing linearly from 2006 to 2011 ($F = 7.813, df = 1, 5, p = 0.038$) at a rate of 0.283 ± 0.101 ; these 2 rates of increasing population density were not significantly different (ANCOVA, $F = 0.141, df = 1, 11, p = 0.714$). MDS visualized the changes in density of small corals (Fig. S2 in the

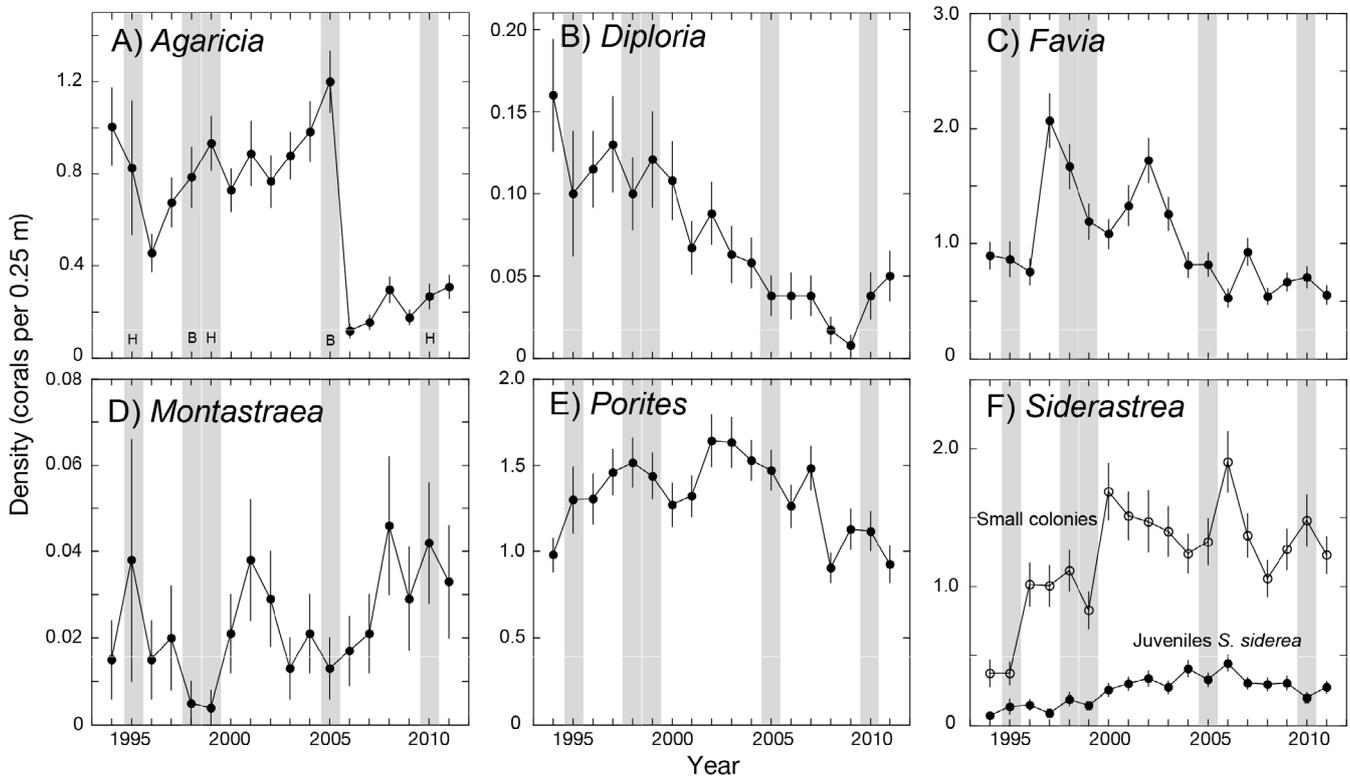


Fig. 5. Density of small corals (≤ 40 mm diameter) by taxon at 5 to 9 m depth between Cabritte Horn and White Point for 18 yr (1994 to 2011). Values pooled among 2 sites (1995), 5 sites (1994, and 1996 to 1998), or 6 sites (1999 to 2011), with $n = 80, 200,$ or 240 quadrats, respectively. Seven taxa account for $>98\%$ of all corals: (A) *Agaricia*, (B) *Diploria*, (C) *Favia*, (D) *Montastraea* (*Orbicella annularis* complex and *M. cavernosa* combined), (E) *Porites*, and (F) *Siderastrea* (open circles) and *S. siderea* (filled circles). Mean \pm SE displayed; gray bars display years affected by bleaching (B) or hurricanes (H) (labeled in panel A only)

Supplement at www.int-res.com/articles/suppl/m489p107_supp.pdf), revealing a shift in community structure between 1994 and 2011 characterized by periods of change between 1995 and 1996 (associated with reductions in density of *Agaricia* and increases in *Siderastrea*), 1996 and 1997 (declines in density of *Favia*), 1999 and 2000 (increases in density of *Siderastrea*), 2005 and 2006 (declines in density of *Agaricia*), and 2007 and 2008 (declines in density of *Porites*).

DISCUSSION

Confronted with substantial threats to ecosystem function arising from GCC and OA (Walther et al. 2002, 2005, Parmesan & Yohe 2003, Doney et al. 2012), research is increasingly focusing on the large-scale biological consequences of these phenomena (Bellard et al. 2012, Doney et al. 2012), and less effort is being spent to study related effects at local scales. Studies of coral reefs reflect this trend, with prominent articles focusing on taxonomic generalities and ecosystem-wide responses rather than the primary analyses on which such studies must be based (e.g. Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011, Zychaluk et al. 2012). A focus on generalities favors oversight of important information revealed by detail-oriented analyses, and obscures just how few decadal-scale data are available to document long-term changes in coral reef community structure (Connell 1997, Schutte et al. 2010). The present study contributes to this detail-oriented niche by describing the community structure of a Caribbean coral reef over 25 yr with annual resolution. Although unusually longevous, this study only dates back to 1987, and therefore began after much of the Caribbean *Acropora* had been killed by white band disease (Aronson & Precht 2001), and the pernicious effects of more than 3 centuries of human exploitation had taken their toll on coral reefs (Jackson 1997). Notwithstanding these important caveats, analyses of the reefs of St. John between 1987 and 2011 reveal that (1) the first decade of change in benthic community structure (Edmunds 2002) was an imperfect predictor of the sequence, magnitude, and type of changes that took place over the following 15 yr; (2) the trajectories of community change are neither similar nor synchronous in 3 habitats; and (3) based on habitat-dependent asynchrony between disturbances and changes in community structure, it is unlikely that the variations in the shallow coral reefs of St. John reflect uniform responses to common stressors.

Contemporary coral reef community structure

Between 1987 and 2011 the reefs of St. John were subjected to a variety of biological and physical disturbances that contributed causally to the changes in community structure that occurred over this period. Periods of seawater warming occurred in 1987, 1998, and 2005 (Text S1 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m489p107_supp.pdf), and were accompanied by coral bleaching. Hurricanes had strong impacts on the region, particularly Hurricanes Hugo in 1989 (Edmunds & Witman 1991, Rogers et al. 1991), Marilyn and Luis in 1995, Lenny in 1999, and Earl in 2010. Hurricanes with smaller impacts affected the region in 1996 (Bertha and Hortense), 1998 (Georges), and 2000 (Debby), and 2010 had the heaviest rainfall in ~30 yr (157 cm at Stn 672551 on St. John; www.sercc.com/cgi-bin/sercc/cliMAIN.pl?vi1980). Other conspicuous phenomena included outbreaks of coral diseases (Edmunds 1991), some of which were locally severe (Miller et al. 2006), and the arrival of the invasive lionfish, *Pterois* spp. in ~2010 (Schofield 2010).

The reefs of St. John are very different now compared with 1987, and although the past 25 yr suggest that further changes in coral reef community structure will occur, the current trends are inconsistent with an immediate future devoid of calcifying scleractinian corals (Pandolfi et al. 2005, Jackson 2008). The PRS with low coral abundance and high cover of macroalgae may serve as an example of the biotically homogenized coral fauna that is beginning to dominate the Florida reef tract (Burman et al. 2012, see also Riegl et al. 2012), with small colonies of eurytopic taxa such as *Agaricia* spp., *Porites* spp., and *Siderastrea siderea* predominating (Burman et al. 2012). While the future of reefs dominated by *Orbicella annularis* appears dismal (Hughes & Tanner 2000, Edmunds & Elahi 2007, Alvarez-Filip et al. 2011), and includes the possibility of local extirpation (Edmunds & Elahi 2007, this study), the present study offers cautious optimism that the reefs of tomorrow are more likely to be characterized by a coral community resembling that found at the PRS than by slime (*sensu* Pandolfi et al. 2005).

When I last described the community dynamics in these habitats (Edmunds 2002), the data spanned 12 yr (1987 to 1998), and included 2 bleaching episodes (1987 and 1998) and 3 major hurricanes (Hugo in 1989, and Luis and Marilyn in 1995). Over this period, the prominent trends were a 56% loss of coral cover at Yawzi Point (45 to 20%), a 34% increase in coral cover at Tektite (32 to 43%), and idiosyncratic

changes in coral cover at the random sites. Macroalgae generally increased in abundance in all 3 habitats and were the dominant benthic category (>50% cover) (sensu Bruno et al. 2009) in one year (1997) at Yawzi Point. While aspects of this earlier study were consistent with the trends for declining coral cover elsewhere in the Caribbean (Hughes 1994, Gardner et al. 2003), spatial heterogeneity in community dynamics, as well as the absence of local disturbances, suggested that regional-scale processes were likely to be important agents of change on these reefs (Edmunds 2002). In this earlier study, increasing coral cover at Tektite was construed as an indication that this area could serve as a refugium (sensu Pielou 1979), from which coral might repopulate adjacent areas (Mumby 1999, Edmunds 2002).

A subsequent demographic analysis of the primary framework-building coral of Yawzi Point—*Orbicella annularis*—revealed the demographic drivers of change in cover of this coral and provided a means to project the population into the future (Edmunds & Elahi 2007). Based on analyses extending 5 yr beyond the initial study (cf. Edmunds 2002), coral cover at Yawzi Point declined more rapidly between 1987 and 1998 than it did between 1998 and 2003, but lessening of the rate of coral loss obscured impending demographic collapse of *O. annularis* (sensu Hughes & Tanner 2000) that projected forward to local extirpation within 50 yr (Edmunds & Elahi 2007). With 8 additional years of monitoring (2004 to 2011), 25 yr of coral reef community dynamics support a more comprehensive interpretation of the recent history of the reef at Yawzi Point and adjacent habitats (cf. Edmunds 2002). Since 2003, coral cover has continued to decline at Yawzi Point, with a further 45% reduction (a decline from 12 to 7% cover) closely matching the losses projected to occur using the size-based matrix model developed using census data from 1998 and 2003 (Fig. 6A in Edmunds & Elahi 2007). Over the same period (i.e. since 2003), the favorable prognosis for the Tektite habitat (Edmunds 2002) reversed, with a decline in coral cover beginning in 2003 and ultimately reducing the coral cover recorded in 2002 by 41%. This loss of coral challenges the notion that Tektite could function as a coral refugium (Edmunds 2002). Just as coral cover at Yawzi Point appeared in 1998 (Edmunds 2002) to be following the same trajectory as coral cover on the degraded reefs of Jamaica (Hughes 1994, Hughes & Tanner 2000), coral cover at Tektite now seems to be following the same trajectory as Yawzi Point with a 16 yr delay. Further, a quarter-century of data reinforces the prominence of spatial heterogeneity in

coral reef community dynamics, both in the case of the south coast of St. John (Edmunds 2000, 2002) and more generally for tropical coral reefs (Connell et al. 1997, Bythell et al. 2000, Osborne et al. 2011, De'ath et al. 2012). In so doing, the present study underscores the limitations of generalizing trends in coral community dynamics as a simple and common response to local and regional disturbances.

Trajectories of change in community structure

The trajectories of change in cover of coral, macroalgae, and CTB differed among habitats in St. John. MDS underscored these contrasting trajectories, with distinct patterns spanning 4 decades at Yawzi Point, more subtle patterns at Tektite that became distinct after 2004, and relatively little variation at the PRS. Although the major disturbances affecting St. John impacted all 3 habitats, the typical consequences of hurricanes (Rogers 1993) and severe bleaching (Glynn 1993, Fitt et al. 2001) did not create spatially coherent signals in their community structure. For instance, while Hurricane Hugo caused large declines in coral cover at Yawzi Point (Edmunds & Witman 1991, Rogers et al. 1991), it had little discernible effect at Tektite, and while bleaching in 2005 was associated with declining coral cover in all 3 habitats, the strongest effects at Tektite were a continuation of a downward trend in coral cover that was initiated by unknown causes in 2003.

Discordant trajectories of change in coral community structure at Yawzi Point, Tektite, and the PRS are inconsistent with a causal origin based solely on the damaging potential of spatially and temporally coherent events. Remarkably, even with 25 yr of data it has proved intractable to establish unequivocal cause-and-effect relationships between local disturbances and the changes in community structure with which they coincide. The complexity of these changes reveals the extent to which the impacts of disturbances are mediated by local history, taxonomic composition, and microenvironment (Done et al. 1991, Witman 1992, Connell 1997, Karlson & Cornell 1999). Not only will these factors determine the community response to local-scale disturbances such as single, compact storms, but they also will influence the impacts of other landscape- and regional-scale disturbances, such as pathogens, rising seawater temperature, and perhaps declining seawater pH. Examples of the unique effects of local history in the present analyses include the positive trajectory of coral cover at Tektite over the first 16 yr of the

study—an outcome that probably reflects the escape of this habitat from the damaging effects of Hurricane Hugo in 1989 (Edmunds 2002). Likewise, the relative consistency of coral cover at the PRS is probably related to the historic absence of dense growths of *Orbicella annularis*, which in this habitat might be a function of poor recruitment due to sediment scour (Chollett & Mumby 2012). At the Yawzi Point and Tektite habitats, it is the loss of this species that has driven the changes in community structure. Not only is *O. annularis* critical in the construction and community ecology of Caribbean reefs (Goreau 1959, Barnes 1973, Knowlton 1992), but it also underpins the maintenance of architectural complexity that promotes biodiversity and ecosystem function (Alvarez-Filip et al. 2011).

Changes in abundance of coral taxa

The present analyses provide a persuasive summary of changes that have taken place in coral reef community structure in St. John, and also reveal that the taxonomic composition of the coral communities has changed. Indirect signs of these changes are inherent in the losses of *Orbicella annularis* at Yawzi Point and Tektite, which have favored the relative abundance of sympatric taxa such as *Porites astreoides*, *P. porites* and *Siderastrea siderea* (P. J. Edmunds unpubl. data). Quantification of these trends was hindered in these 2 habitats by the use of 1 m² photoquadrats, which capture less detail than the 0.25 m² photoquadrats that were used at the PRS. The resolution of the photoquadrats at the PRS allowed 8 coral genera to be resolved with confidence, with these data demonstrating that the coral community has changed significantly in composition. Although these effects are inevitably subtle because of the small amounts of coral present (<4.5% cover), they reveal that a leading cause of the change in taxonomic composition was *Agaricia* spp., which declined in abundance after 1997 and again after 2005. Both declines were coincident with upward thermal anomalies in 1998 and 2005 (Hoegh-Guldberg 1999, Donner et al. 2005) and are consistent with the high thermal sensitivity of this genus (Gates 1990, Aronson et al. 2000, Robbart et al. 2004).

Shifts in the composition of the coral communities in St. John are better revealed by the direct counts of small corals (≤ 40 mm diameter) at 5 to 9 m depth than the photoquadrats at the PRS. Although the efficacy of the photoquadrats is limited by low coral cover, direct counts underwater by eye afford a greater

opportunity of detecting the smallest corals, which might be obscured by macroalgae. Although small corals and the benthic community structure at the PRS were not quantified in identical areas, the *in situ* surveys for small corals took place in adjacent areas and within a depth range of 5 to 9 m. The abundance of small corals and coral cover at the PRS were correlated positively for the 18 yr between 1992 and 2011 ($r = 0.548$, $df = 16$, $p = 0.019$), suggesting that fluctuations of small corals were indeed playing an important role in determining the percentage cover of scleractinian corals in adjacent areas. Previously, a test of the same hypothesis substituting space (i.e. sites) for time did not detect an association between the density of juvenile corals and coral cover (Edmunds 2000), but such a test is less effective than the present analysis that utilized 6 sites in most years and directly captured interannual variation over nearly 2 decades. Furthermore, initial results (4 yr) from a new effort to quantify coral recruitment using settlement tiles in Lameshur Bay demonstrates that the recruitment of poritids is correlated positively with the density of small *Porites* (≤ 40 mm diameter) on adjacent reef surfaces (P. J. Edmunds unpubl. data). This outcome suggests that the abundance of small corals in St. John is determined by recruitment that varies among years.

When the change in abundance of small corals was separated by genus, the trajectories differed and contained multiple reversals (i.e. increases followed by declines, and declines followed by increases). For example, *Agaricia* was at times the second-most abundant genus of small corals (after *Porites*), but underwent the largest reduction in abundance during the study and then began to recover in population size. Remarkably, the present data show that the rates of population growth for *Agaricia* were statistically indistinguishable before and after the bleaching disturbance of 2005, and in this regard, *Agaricia* displays strong ecological stability (sensu Holling 1973). In contrast, *Diploria* staged a protracted decline in abundance even while overall population size was increasing on nearby reefs (Edmunds 2010), and *Favia* initially doubled in density between 1996 and 1997, but then staged a consistent population decline interspersed with 2 transitory increases in density. Juvenile '*Montastraea*' were rarely encountered (≤ 0.183 corals per 0.25 m²), and while they changed in density throughout the study, the changes did not display a clear directional trend. Although the absolute densities of '*Montastraea*' juveniles were low, the values were relatively high given the poor prognosis for *Orbicella annularis* (Edmunds & Elahi 2007) and the

exceptionally low rate of recruitment of *O. annularis* complex throughout the Caribbean over the past 30 yr (Edmunds et al. 2011).

The density of juvenile *Porites* increased for about half the study, as might be predicted by its tendency to function as an ecological winner (Green et al. 2008, Edmunds 2010), but the apparent success of this size class reversed in the second half of the study. Finally, *Siderastrea* maintained strong population growth throughout the study, both for all small colonies (i.e. *S. radians* and *S. siderea*) and for juvenile *S. siderea* alone. This distinction is important, as small *S. radians* (≤ 4 cm diameter) are sexually mature (i.e. they are adults; Soong 1993), and their long life span (Edmunds 2007) and resilient phenotype (Lirman et al. 2002) complicate contrasts with equivalent-sized colonies of other taxa that are functionally juvenile (Soong 1993). Together, the aforementioned trends of changing population sizes of small corals are important, because they reveal how differential success of functionally unequal corals fuels trajectories of change in overall coral cover. As coral genera display multiple bouts of success and failure over time (as inferred from their abundance), thereby demonstrating how short-term winners can become long-term losers (and vice versa) (Brown & Phongsuwan 2012), the community response to disturbances will depend on the timing of the disturbances relative to the comingled trajectories of population dynamics. These effects may be central to understanding how similar disturbances result in different responses in coral communities in adjacent reef habitats, as is described in the present study. Perhaps it is the maintenance of a shifting mosaic of differential abundances of functionally unequal corals that contributes to ecological stability (sensu Holling 1973) in the biotically homogenized coral faunas that now appear to be emerging from more than 200 yr of the Anthropocene epoch.

The future of coral reefs off St. John

In ecological investigations, it has been argued that the past is the key to understanding the future (Precht & Miller 2007, Petit et al. 2008, Pardi & Smith 2012), with the validity of this refrain resting on the assumption that the response of biota to future conditions is revealed by their responses to previous conditions. As the planet continues to warm and atmospheric $p\text{CO}_2$ increases at a rate unprecedented in the past 800 000 yr (Lüthi et al. 2008), this assumption may be tested in unforeseen ways as novel ecological

winners (and losers) (sensu Loya et al. 2001) emerge from a new physicochemical landscape. Nevertheless, for the shallow reefs of St. John, the past 25 yr provide the best means to project how these coral reefs will change in the future. Here, I focused on the recent abundances of benthic taxa as a means to project community structure into the future. This approach has important limitations, including insensitivity to impending demographic collapse (Hughes 1984, Hughes & Tanner 2000, Edmunds & Elahi 2007). Nevertheless, it provides a simplified insight into how the community will change in the near future. Alternative approaches, such as size-based matrix models (Hughes 1984) and multivariate autoregressive models (Ives et al. 2003) are better suited to population projection.

Assuming the past is the best predictor of the near future, and that contemporary trends in changing coral reef community structure (as well as the factors driving them) are sustained, the recent linear portions of the trajectories of changing coral cover at Yawzi Point (1999 to 2011), Tektite (2002 to 2011), and the PRS (1992 to 2011) suggest that the 3 habitats will display dissimilar dynamics in the next few decades. Coral cover at Yawzi Point declined linearly ($p < 0.001$) at $0.5 \pm 0.1\% \text{ yr}^{-1}$ between 1999 and 2011, suggesting that coral cover could approach 0% in ~ 14 yr; at Tektite, coral cover declined linearly ($p < 0.001$) at $2.4 \pm 0.4\% \text{ yr}^{-1}$ between 2002 and 2011, suggesting that coral cover could approach 0% in ~ 12 yr; and at the PRS, coral cover remained independent of time ($p = 0.139$), and therefore, might persist at the current low level ($\sim 4\%$). Interestingly, the cover of macroalgae reached 25 to 37% in all 3 habitats by 2011, and although it has varied extensively over the past decade, the consistently high cover of this group reinforces the likelihood that these areas have undergone a phase change to macroalgal dominance (see Rogers & Miller 2006). In the absence of a recovery of herbivore populations, such as the echinoid *Diadema antillarum*, which may require >1000 yr to recover to its former population density in this locality (D. R. Levitan et al. unpubl.), it seems unlikely that large declines in macroalgal cover will occur on these reefs.

The extent to which linear projections of coral cover reflect reality is unknown, but a leading reason to suspect that the reality will differ is the likelihood that changing coral cover is accompanied by shifts in the relative abundances of coral taxa (Aronson et al. 2005, van Woesik et al. 2011). This concept has been popularized as the 'winners and losers' of environmental assaults on coral reefs (Loya et al. 2001, van

Woesik et al. 2011), and has gained support from signs that some corals are resistant to environmental assaults (Fabricius et al. 2011), while others appear to have the capacity to acquire resistance (Jones et al. 2008, Maynard et al. 2008). Clearly, if coral taxa with differing abilities to resist environmental assaults change in relative abundances, then reefs with a greater proportion of resistant taxa will be less likely to decline in coral cover than reefs dominated by susceptible taxa. As susceptible corals are culled from reef communities by disturbances, further declines in coral cover—even if coral cover has declined to historically low levels—will be less likely to occur than the recent trajectories of change might suggest. In such cases, the recent past might be a poor indicator of future performance, and linear projections of changes in coral cover will prove to be unreliable indicators of the future. While a quarter-century of data in the present study provide little optimism that reefs dominated by *Orbicella annularis* will persist much more than a couple of decades, the community dynamics of the PRS have proved remarkably persistent through multiple disturbances. Perhaps it is this reef habitat that provides the most effective glimpse of what coral reefs in the future might look like.

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LITERATURE CITED

- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc R Soc Lond B Biol Sci* 276: 3019–3025
- Alvarez-Filip L, Dulvy NK, Côté IM, Watkinson AR, Gill JA (2011) Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story? *Glob Change Biol* 17:2470–2477
- Aronson RB, Precht WF (2000) Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnol Oceanogr* 45:251–255
- Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25–38
- Aronson RB, Precht WF, Macintyre IG, Murdoch TJ (2000) Coral bleach-out in Belize. *Nature* 405:36
- Aronson RB, Macintyre IG, Lewis SA, Hilbun NL (2005) Emergent zonation and geographic convergence of coral reefs. *Ecology* 86:2586–2600
- Barnes DJ (1973) Coral reef project papers in memory of Dr. Thomas F. Goreau. 12. Growth in colonial scleractinians. *Bull Mar Sci* 23:280–298
- Bellard C, Bertelsmeier C, Leadley P, Wilfried T, Courchamp F (2012) Impacts of climate change on the future biodiversity. *Ecol Lett* 15:365–377
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Brown BE, Phongsuwan N (2012) Delayed mortality in bleached massive corals on intertidal reef flats around Phuket, Andaman Sea, Thailand. *Phuket Mar Biol Cent Res Bull* 71:43–48
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent and subregional comparisons. *PLoS ONE* 8:e711
- Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VG (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484
- Budd AF, Fukami H, Smith ND, Knowlton N (2012) Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zool J Linn Soc* 166:465–529
- Burman SG, Aronson RB, van Woesik R (2012) Biotic homogenization of coral assemblages along the Florida reef tract. *Mar Ecol Prog Ser* 467:89
- Burrows MT, Schoeman DS, Buckley LB, Moorea P and others (2011) The pace of shifting climate in marine terrestrial ecosystems. *Science* 334:652–655
- Bythell JC, Hillis-Starr ZM, Rogers CS (2000) Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Mar Ecol Prog Ser* 204:93–100
- Chollett I, Mumby PJ (2012) Predicting the distribution of *Montastrea* reefs using wave exposure. *Coral Reefs* 31:493–503
- Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth
- Collette BB, Earle A (1972) Results of the Tektite program: ecology of coral reef fishes. *Los Angeles Co Nat Hist Mus Sci Bull* 14:180
- Connell JH (1978) Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. *Science* 199:1302–1310
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Proc 8th Int Coral Reef Symp* 1:9–22
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- Crutzen PJ (2002) Geology of mankind. *Nature* 415:23
- De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci USA* 109: 17995–17999

- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132
- Done TJ, Dayton PK, Dayton EA, Steger R (1991) Regional and local variability in recovery of shallow coral communities: Moorea, French Polynesia and central Great Barrier Reef. *Coral Reefs* 9:183–192
- Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO₂ problem. *Annu Rev Mar Sci* 1:169–192
- Doney SC, Ruckelshaus M, Duffy JE, Barry JP and others (2012) Climate change impacts on marine ecosystems. *Annu Rev Mar Sci* 4:11–37
- Donner SD, Skirving WJ, Little CM, Little CM, Oppenheimer M, Hoegh-Guldberg O (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob Change Biol* 11:2251–2265
- Dudgeon SR, Aronson RB, Bruno JF, Precht WF (2010) Phase shifts and stable states on coral reefs. *Mar Ecol Prog Ser* 413:201–216
- Edmunds PJ (1991) Extent and effect of black band disease on a Caribbean reef. *Coral Reefs* 10:161–165
- Edmunds PJ (2000) Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Mar Ecol Prog Ser* 202:113–124
- Edmunds PJ (2002) Long-term dynamics of coral reefs in St. John US Virgin Islands. *Coral Reefs* 21:357–367
- Edmunds PJ (2007) Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. *Mar Ecol Prog Ser* 341:1–13
- Edmunds PJ (2010) Population biology of *Porites astroides* and *Diploria strigosa* on a shallow Caribbean reef. *Mar Ecol Prog Ser* 418:87–104
- Edmunds PJ (2013) Virgin Islands National Park Coral Reef: Decadal-scale changes in community structure from 1987 to 2011, doi:10.5063/AA/knb-csun-usvi.10700, (available at <http://knb.ecoinformatics.org/knb/metacat/knb-csun-usvi.10700.1/knb>)
- Edmunds PJ, Elahi R (2007) The demographic of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecol Monogr* 77:3–18
- Edmunds PJ, Witman JD (1991) Effect of Hurricane Hugo on the primary framework of a reef along the south shore of St. John, US Virgin Islands. *Mar Ecol Prog Ser* 78:201–204
- Edmunds PJ, Ross CLM, Didden C (2011) High but localized recruitment of *Montastrea annularis* complex in St. John, United States Virgin Islands. *Coral Reefs* 30:123–130
- Fabricius KE, Langdon C, Uthicke S, Humphrey C and others (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Clim Change* 1:165–169
- Fitt WK, Brown BE, Warner ME, Dunne RP (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20:51–65
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Gates RD (1990) Seawater temperature and sublethal coral bleaching in Jamaica. *Coral Reefs* 8:193–197
- Ginsburg RN (ed) (1994) *Proc Colloquium Global Aspects of Coral Reefs: Health, Hazards, and History*. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL
- Glynn PW (1993) Coral reef bleaching: ecological perspectives. *Coral Reefs* 12:1–17
- Goreau TF (1959) The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* 40:67–90
- Green DH, Edmunds PJ, Carpenter RC (2008) Increasing relative abundance of *Porites astroides* on Caribbean reefs mediated by an overall decline in coral cover. *Mar Ecol Prog Ser* 359:1–10
- Harvell D, Aronson R, Baron N, Connell J and others (2004) The rising tide of ocean diseases: unsolved problems and research priorities. *Front Ecol Environ* 2:375–382
- Hatcher BG (1984) A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. *Coral Reefs* 3:199–204
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS and others (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742
- Holling CS (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23
- Hughes TP (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. *Am Nat* 123:778–795
- Hughes TP (1992) Monitoring of coral reefs: a bandwagon. *Reef Encounter* 11:9–12
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551
- Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81:2250–2263
- Hughes TP, Reed DC, Boyle MJ (1987) Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J Exp Mar Biol Ecol* 113:39–59
- Hughes TP, Szmant AM, Steneck R, Carpenter RC, Miller S (1999) Algal blooms on coral reefs: What are the causes? *Limnol Oceanogr* 44:1583–1586
- Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Ives AR, Dennis B, Cottingham KL, Carpenter SR (2003) Estimating community stability and ecological interactions from time-series data. *Ecol Monogr* 73:301–330
- Jackson JBC (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am Nat* 111:743–767
- Jackson JBC (1997) Reefs since Columbus. *Coral Reefs* 16(Suppl):23–32
- Jackson JBC (2008) Ecological extinction and evolution in the brave new ocean. *Proc Natl Acad Sci USA* 105:11458–11465
- Jones AM, Berkelmans T, van Oppen MJ, Mieog JC, Sinclair W (2008) A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization. *Proc R Soc Lond B Biol Sci* 275:1359–1365
- Karlson RH, Cornell HV (1999) Integration of local and regional perspectives on the species richness of coral assemblages. *Am Zool* 39:104–112
- Karlson RH, Hurd LE (1993) Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs* 12:117–125

- Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ and others (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob Ecol Biogeogr* 21:393–404
- Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. *Am Zool* 32:674–682
- Kohler KE, Gill SM (2006) Coral point count with excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci* 32: 1259–1269
- Kroeker KJ, Kordas RL, Crim RN, Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol Lett* 13: 1419–1434
- Lee CC, Lee EL, Bunt JS (1975) Distribution of biomass in a coral reef transect. *Los Angeles Co Nat Hist Mus Sci Bull* 20:69–103
- Lighty RG (1982) Fleishy-algal domination of a modern Bahamian Barrier reef: example of an alternate climate reef community. In: *Proc 4th Int Coral Reef Symp*, Manila 1:722
- Lirman D, Manzello D, Maciá S (2002) Back from the dead: the resilience of *Siderastrea radians* to severe stress. *Coral Reefs* 21:291–292
- Loya Y, Sakai K, Yamazato K, Nakano Y and others (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4: 122–131
- Lüthi D, Le Floch M, Bereiter B, Blunier T and others (2008) High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature* 453: 379–382
- Maynard JA, Baird AH, Pratchett MS (2008) Revisiting the Cassandra syndrome; the changing climate of coral reef research. *Coral Reefs* 27:745–749
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18: 357–367
- Miller J, Waara R, Muller R, Rogers C (2006) Coral bleaching and disease combine to cause extensive mortality on reefs in US Virgin Islands. *Coral Reefs* 25:418
- Moore JE, Barlow J (2011) Bayesian state-space model of fin whale abundance trends from a 1991–2008 time series of line-transect surveys in the California Current. *J Appl Ecol* 48:1195–1205
- Mumby PJ (1999) Bleaching and hurricane disturbances to populations of coral recruits in Belize. *Mar Ecol Prog Ser* 190:27–35
- Mumby PJ (2009) Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28: 761–773
- Mumby PJ, Steneck RS, Hastings A (2012) Evidence for and against the existence of alternate attractors on coral reefs. *Oikos* 122:481–491
- Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- O'Brien SJ, Evermann JF (1988) Interactive influences of infectious disease and genetic diversity in natural populations. *Trends Ecol Evol* 3:254–259
- Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009). *PLoS ONE* 6:e17516
- Pandolfi JM, Jackson JBC, Baron N, Bradbury R and others (2005) Are the US coral reefs on the slippery slope to slime? *Science* 307:1725–1726
- Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. *Science* 333:418–422
- Pardi MI, Smith FA (2012) Paleoecology in an era of climate change: how the past can provide insights into the future. In: Louys J (ed) *Paleontology in ecology and conservation*. Springer Earth System Sciences, Berlin, p 93–116
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37: 637–669
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Petit RJ, Hu FS, Dick CW (2008) Forests of the past: a window to future changes. *Science* 320:1450–1452
- Pielou EC (1979) *Biogeography*. Wiley, New York, NY
- Precht WF, Miller SL (2007) Ecological shifts along the Florida Reef Tract: the past as a key to the future. In: Aronson RB (ed) *Geological approaches to coral reef ecology*. Springer, New York, NY, p 237–312
- Quinn GP, Keough MJ (2003) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Randall JE (1961) Tagging reef fishes in the Virgin Islands. *Proc Gulf Caribb Fish Inst* 14:210–241
- Richardson AJ, Brown CJ, Brander K, Bruno JF and others (2012) Climate change and marine life. *Biol Lett* 8: 907–909
- Riegl BM, Sheppard CR, Purkis SJ (2012) Human impact on atolls leads to coral loss and community homogenization: a modeling study. *PLoS ONE* 7:e38396
- Robbart ML, Peckol P, Scordilis SP, Curran HA, Brown-Sarcino J (2004) Population recovery and differential heat shock protein expression for the corals *Agaricia agaricites* and *A. tenuifolia* in Belize. *Mar Ecol Prog Ser* 283:151–160
- Rogers CS (1993) Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. *Coral Reefs* 12: 127–137
- Rogers CS (1999) Sampling may be haphazardous to your reef monitoring program. In: Maragos JE, Grober-Dunsmore R (eds) *Proc Hawaii Coral Reef Monitoring Workshop*. Division of Aquatic Resources, Hawaii State Government, Honolulu, HI, p 57–64
- Rogers CS, Beets J (2001) Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the US Virgin Islands. *Environ Conserv* 28: 312–322
- Rogers CS, Miller J (2006) Permanent 'phase shifts' or reversible declines in coral cover? Lack of recovery of two coral reefs in St. John, US Virgin Islands. *Mar Ecol Prog Ser* 306:103–114
- Rogers CS, Teytaud R (1988) Marine and terrestrial ecosystems of the Virgin Islands National Park and Biosphere Reserve. *Biosphere Reserve Rep* 29:1–112
- Rogers CS, McLain LN, Tobias CR (1991) Effects of Hurricane Hugo (1989) on a coral reef in St. John, USVI. *Mar Ecol Prog Ser* 78:189–199
- Rogers CS, Miller J, Muller EM, Edmunds PJ and others (2008) Ecology of coral reefs in the US Virgin Islands. In:

- Riegl BM, Dodge RE (eds) Coral reefs of the USA. Springer, Dordrecht, p 303–373
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA and others (2008) Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE* 3:e1548
- Schofield PJ (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1928]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. *Aquat Invas* 5: S117–S122
- Schutte VG, Selig ER, Bruno JF (2010) Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Mar Ecol Prog Ser* 402:115–122
- Sheppard CRC, Harris A, Sheppard ALS (2008) Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. *Mar Ecol Prog Ser* 362:109–117
- Soong K (1993) Colony size as a species character in massive reef corals. *Coral Reefs* 12:77–83
- Steffen W, Crutzen PJ, McNeill JR (2007) The Anthropocene: Are humans now overwhelming the great forces of nature? *Ambio* 36:614–621
- van Woesik R, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and the losers a decade after coral bleaching. *Mar Ecol Prog Ser* 434:67–76
- Walther GR, Post R, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Walther GR, Berger S, Sykes MT (2005) An ecological ‘footprint’ of climate change. *Proc R Soc Lond B Biol Sci* 272:1427–1432
- Witman JD (1992) Physical disturbance and community structure of exposed and protected reefs: a case study from St. John, US Virgin Islands. *Am Zool* 32:641–654
- Woodruff DS (2001) Declines of biomes and biotas and the future of evolution. *Proc Natl Acad Sci USA* 98: 5471–5476
- Żychaluk K, Bruno JF, Clancy D, McClanahan TR, Spencer M (2012) Data-driven models for regional coral-reef dynamics. *Ecol Lett* 15:151–158

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